Designing wetlands for amphibians: the importance of predatory fish and shallow littoral zones in structuring of amphibian communities

Deni Porej[1,*] and Thomas E. Hetherington[2]

[1]*The Nature Conservancy, 6375 Riverside Drive, Suite 50, Dublin, OH 43207, USA;* [2]*Department of Evolution, Ecology and Organismal Biology, 1735 Neil Avenue, The Ohio State University, Columbus, OH 43210, USA;* *Author for correspondence (e-mail: dporej@tnc.org; phone: +1-614-717-2770; fax: +1-614-717-2777)*

Abstract

Under section 401 and section 404 of the Clean Water Act, permission to degrade existing natural wetlands in the USA may be conditional on restoring or creating 'replacement' wetlands. Success of wetland mitigation efforts in adequately replacing lost wildlife habitats depends on our good understanding of key ecological attributes that affect the structure of wetland faunal communities. We examined the effects of the presence of predatory fish, shallow vegetated littoral zone, emergent vegetation cover, wetland age and size on amphibian diversity in 42 replacement wetlands located in the Ohio's North Central Tillplain ecoregion. We recorded 13 species of pond-breeding amphibians, and the average local species richness (α-richness) was 4.2 ± 1.7 species per site (range 1–7). There is strong evidence for the positive association between amphibian species richness and presence of a shallow littoral zone, and the negative association with presence of predatory fish. There was no evidence for the association between species richness and age, size, amount of forest cover within 200 m, nor the amount of emergent vegetation cover at the study sites. It is estimated that local species richness in wetlands with shallows was 1.76 species higher on average than in wetlands without shallows (95% CI from 0.75 to 2.76). The presence of predatory fish was associated with an average reduction in species richness by an estimated 1.21 species (95% CI from 0.29 to 2.11). Replacement wetlands were placed in areas with little or no existing forest cover, and amphibian species associated with forested wetlands were either rare (eastern newt, spotted salamander) or not present at all (marbled salamander, wood frog). In addition, we surveyed all replacement wetlands constructed under section 401 in Ohio since 1990, and found that predatory fish were present in 52.4% of the sites and that shallows were absent from 42.7% of the sites. Our results indicate that current wetland replacement practices could have a negative effect on the amphibian diversity within our region.

Introduction

Under section 404 and section 401 of the Federal Water Pollution Control Act and subsequent amendments (The Clean Water Act), the approval to fill, drain or otherwise degrade a wetland in the USA may be conditional on restoring, creating or enhancing wetlands to compensate for any unavoidable loss in wetland area and function. Replacement ('mitigation') wetlands are built with

the intent to replace all of the functions of lost wetlands, including storm water detention, water purification, nutrient cycling, ground water recharge and wildlife habitat (National Wetland Policy Forum 1988; US Department of the Army and US Environmental Protection Agency 1990). However, replacement of wildlife habitat is usually not one of the functions monitored or regulated (National Research Council 1995, 2001). When wetland assessments involve animals, the primary consideration is waterfowl, other birds or identifiable endangered/threatened species (National Research Council 2001).

Pond-breeding amphibians are an integral part of wetland ecosystems, but amphibians usually do not fall into any of the above categories. As a consequence replacement or creation of quality amphibian habitat is usually not one of the goals of wetland replacement. Amphibians in the American Midwest have suffered major loss of habitat due to the conversion of nearly 90% of pre-settlement wetlands to agricultural uses (Dahl 1990). It is therefore critical that, whenever possible, we manage remaining wetlands in a manner consistent with amphibian conservation and use every opportunity to re-create quality amphibian habitat (Leja 1998). Success of wetland mitigation efforts in adequately replacing lost ecosystems, and perhaps even in creating higher quality habitats than the impacted wetlands, is dependent on a thorough understanding of the key ecological attributes important in structuring the composition of wetland-dependent faunal communities.

A National Research Council study (National Research Council 2001) concluded that hydrological variability is often not established in created/ restored replacement wetlands, and that concerns about not meeting the hydrological criteria used to define wetlands in the permitting process often encourages construction of permanently flooded, open water wetlands. Studies of replacement wetlands in the Midwest (Galatowitsch and van der Valk 1996; Gallihugh 1998; Robb 2000; Porej 2003), and elsewhere around the USA (Campbell 1996; Magee et al. 1996), confirm this trend. In addition, average bank slopes of replacement wetlands were reported to be significantly steeper compared to natural reference wetlands in several studies (Fenessy 1997; Gallihugh 1998). Replacement of diverse natural wetlands with permanent open water wetlands may have a significant negative impact on wetland-dependent fauna. Wetlands with permanent standing water have more amphibian predators, including odonates, dytiscid beetles and predatory fish (e.g., Smith 1983; Woodward 1983; Skelly 1992, 1996; Wellborn et al. 1996). Several studies suggest that fish predation affects the structure of amphibian communities (Hecnar and M'Closkey 1997; Adams 1999; Smith et al. 1999). Furthermore, steep bank slopes preclude the formation of a shallow littoral zone, which provides suitable egg laying, foraging and refugia sites for pond-breeding amphibians.

We investigate how the presence of predatory fish and the absence of a shallow littoral zone affect the structure of amphibian communities of replacement wetlands in central Ohio. We predicted that the presence of a vegetated shallow littoral zone would have a positive effect on species richness, whereas the presence of predatory fish would be associated with a decrease in species richness. We predicted differential species-specific responses to these two variables due to differences in larval behavior (e.g. Woodward 1983; Petranka et al. 1987) and larval palatability (Kats et al. 1988) among the species studied.

While the focus of our research was on the wetlands constructed for regulatory purposes, our study is relevant to natural resource agencies which are involved in wetland creation/restoration, and numerous voluntary-participation programs that offer technical and financial support to private landowners and farmers in the United States to encourage them to restore and preserve wetlands on their property (e.g., Conservation Reserve Program and Wetlands Reserve Program)

Study sites

Amphibian survey sites

In 2000, we compiled all available information on wetland replacement projects located within the North Central Tillplain ecoregion of central Ohio. Access permission was obtained for 42 wetlands, and these sites were included in our study. In 2001, we sampled 38 wetlands. In 2002, all but one site was re-sampled, and three new sites were added for a total of 41 sites. Based on the ongoing file review, we estimate that this number represents over 85%

of all the wetlands constructed under individual section 401permits within this region.

Data on the surrounding landscape composition were obtained from National Land Cover Database and National Wetland Inventory maps using ARC GIS applications (Environmental Systems Research Institute 1990). Data were verified by field reconnaissance and review of aerial photographs of the wetlands and the surrounding areas taken in late 1990s. The dominant landuse within our study area is row-crop agriculture, which in combination with fallow fields composed of 60–91% of the landcover within 1 km radius of individual study sites. Although 90% of Ohio was forested in pre-European settlement era, forest landcover is now generally < 10% across the entire ecoregion (8–17% within the 1 km radius). The primary land use within the 200 m of the sites is row-crop agriculture (average 49.2 ± 3.1%, range 15–79%) with scattered woodlots (average forest landcover 24.8 ± 2.1%, range 8–62%). Although the composition of the surrounding landscape is one of the key factors in structuring the amphibian communities (Laan and Verboom 1990; Koloszvary and Swihart 1999; Knutson et al. 1999, 2000; Lehtinen et al. 2001; Porej 2004; Porej et al. 2004), the relative uniformity of the landscape surrounding our study sites allowed us to focus on examining the association between amphibian diversity and several local, within-wetlands factors (wetland age, size, presence of predatory fish and shallow littoral zones).

Other replacement wetlands in Ohio

In order to document the current trends in the construction of replacement wetlands, in 2002–2003 we recorded basic habitat characteristics (size, presence of shallows and predatory fish) of all replacement wetlands constructed under section 401 in Ohio since 1990. We visited 75 sites in addition to 42 sites at which we carried out detailed amphibian surveys.

Methods

Within-wetland habitat characteristics

Bank slopes were calculated using elevation data collected along transects extending into the wetland and running parallel to the long and short axis of the wetland. Each transect was 15 m long and divided into three 5 m sections. 'Shallows' are defined as areas with bank slopes of less than 15:1 over each of the three 5 m sections of the 15 m transect and vegetation cover of over 50%. Total area and % area covered by different vegetation types were calculated from vegetation maps made from available recent aerial photographs, GPS mapping, and field measurements collected using a Bushnell Yardage Pro® 500 Laser Rangefinder.

Sampling techniques

Amphibian surveys were conducted once during each of the three periods: 15 March–15 April, 15 May–10 June, and 20 June–10 July in 2001 and 2002. Each amphibian survey consisted of deployment of aquatic funnel traps, dip-netting, and visual surveys. In addition, four chorusing surveys were conducted during the last week of March, April, May and June, following the recommendations of the Ohio Frog and Toad Calling Survey (http://www.dnr.state.oh.us/wildlife/resources/survey/index.html).

Aquatic funnel traps were made of aluminum and fiberglass window screen and had funnels at both ends that tapered from a 20 cm diameter to a 4 cm entrance hole. We followed recommendations by Adams et al. (1997) and placed two traps for the first 25 m^2 of a particular habitat unit (e.g., open water, emergent, scrub–shrub), and added one more trap each time the area of the habitat unit doubled (e.g., a 100 m^2 habitat patch received four traps). Habitats within the wetlands were classified as open water (which sometimes included submerged vegetation), emergent, shrub–scrub, and forested. The majority of study sites (38 out of 42) consisted only of emergent vegetation habitat (2–96% of the total wetland area) and open water (20–90% of the total wetland area). Four sites had a small scrub–shrub component (3–8% of the total wetland area), and three study sites had a small forested component (3–7% of the total wetland area) composed of mostly dead trees flooded during the wetland construction. Traps were retrieved approximately 24 h after deployment.

Dipnetting was done concurrently with funnel trapping at each wetland during each of the three sampling periods. Dip net sweeps were made in all

habitat types for a minimum of 30 min per habitat type (Shaffer et al. 1996). Woody debris and other substrate materials were manually collected and searched for eggs and larvae. All adult and juvenile amphibians encountered while deploying or retrieving traps were hand captured (or the best effort was made), identified and released.

Fish were captured in funnel traps and during dipnetting. Fish were captured in at least two survey periods per year in all wetlands that we classified as having predatory fish. We followed Hecnar and M'Closkey's (1997) classification of fish into predatory (centrarchids, eocids and salmonids) and non-predatory categories (cyprinids and mud minnows).

Chorusing surveys began 1.5 h after dusk and lasted 15 min at each site. Surveys concluded at midnight, and three to six sites were visited per night depending on the travel time between sites. Chorusing intensity was ranked from 0 to 3 as follows: no calls recorded (0), single male calling (1), multiple, but non-overlapping calls (2), and multiple, overlapping calls (3).

Capture of larvae or emigrating juveniles using funnel traps, dipnetting or captures during visual surveys was required for us to consider a species 'present' at the site for the purposes of this study. The only exception is Blanchard's cricket frog for which we have recorded level three choruses at five sites, but caught tadpoles in only three sites. We considered Blanchard's cricket frog to be present at all five sites. Except for the above mentioned three localities for Blanchard's cricket frog, chorusing surveys did not add any new records, as we have captured tadpoles of all species for which we have recorded choruses. Tadpoles of American toads (*Bufo americanus americanus*) and Fowler's toads (*Bufo fowleri*) are undistinguishable, and we separated these two species based on chorusing surveys and captures of adults.

Statistical analyses

In order to calculate species turnover between the two study years we constructed a species-locality matrix for each year, and recorded the number of 'unique' records (i.e., species recorded at a site in 2001 but not in 2002) for both 2001 and 2002. We then calculated the turnover percentage by dividing the sum of unique species-location records for 2001 and 2002 by the total number of species-locality records in both years and multiplying that number by 100. A *G*-test with William's correction was used to test whether the distribution of individual species was significantly different between years.

We analyzed the association between the presence of shallows and predatory fish (as effects) with local amphibian species richness (as a response variable) using a univariate general linear model (GLM, SPSS 1998) with % forest landcover within 200 m (%FOR200), % emergent vegetation cover (%EMERG), wetland age and size as covariates. We used Levene's test of equality of error variances to check for model assumptions regarding equal error variance across groups.

Associations between the presence of individual species, presence of predatory fish, and presence of shallows were investigated using the 3-way *G*-test (Brown and Downhower 1988). This test allowed us to partition G_T into components that corresponded to 3 pairwise (2-way) comparisons between these three binary variables and one 3-way joint interaction component. We had a sufficient sample size to test for species-specific effects of the study variables for nine species. 'Species × Fish' and 'Species × Shallow' are tests of the hypotheses that the presence of a particular species is independent of the presence of fish and the presence of shallows, respectively. The 'Shallow × Fish' value was constant because it was determined by our initial choice of study sites (see Study sites). Finally, 'Species × Fish × Shallow' tested for joint interaction among the three factors. Each component was compared to the chi-squared distribution to test for independence. Averages are followed by ± SE, unless noted otherwise. All analyses were performed using Minitab V.12.2 (Minitab Inc., 1998), except the 3-way *G*-test, which was done in Microsoft Excel.

Results

Study sites

A majority of our study sites were permanent wetlands (81%), including all wetlands without a shallow littoral zone. There were no significant differences in the mean age ($F_{(3,38)} = 2.1$, $p = 0.11$), size ($F_{(3,38)} = 2.0$, $p = 0.12$) or %FOR200 ($F_{(3,38)} = 0.67$, $p = 0.57$) among wetlands grouped based on the presence of shallows and predatory fish (Table 1). Wetlands with shallows had significantly

higher % emergent vegetation coverage than wetlands without shallows (95% CI of the difference 8.7–35.0%).

Species recorded

We recorded 13 species of pond-breeding amphibians during the 2001–2002 field seasons (Table 2). Average local species richness (α-richness) was 4.2 ± 1.7 species per site (range 1–7). We collected 168 species-locality records in 2001, and 164 in 2002, with species turnover between years of 3.9%. None of the study species differed in presence/absence at study sites between years based on G-tests with William's correction. Therefore, in the following analyses, data from both years are pooled, and species are considered as present at the site if larvae were recorded in any of the two study years.

Effects of shallows and predatory fish on local amphibian species richness

There is strong evidence for the association between local amphibian species richness (Figure 1) and both SHALLOW ($F_{(1,35)} = 12.53$, $p < 0.001$) and FISH ($F_{(1,35)} = 7.21$, $p = 0.011$). There was no evidence for the association between species richness and AGE ($F_{(1,35)} = 1.42$, $p = 0.24$), SIZE ($F_{(1,35)} = 1.02$, $p = 0.31$), %FOR200 ($F_{(1,35)} = 0.19$, $p = 0.66$) nor %EMERG ($F_{(1,35)} = 1.36$, $p < 0.25$). None of the interaction terms in the model were statistically significant (all $p > 0.2$). It is estimated that local species richness in wetlands with shallows was 1.76 species higher on average than in wetlands without shallows (95% CI from 0.75 to 2.76). The presence of predatory fish was associated with an average reduction in species richness by an estimated 1.21 species (95% CI from 0.29 to 2.11). Wetlands with predatory fish and without shallows

Table 1. Characteristics of 42 study replacement wetlands grouped based on the presence of shallows (SHALLOWS) and predatory fish (FISH).

Group	N	Permanent	Age (years)	Size (ha)	%FOR200	%EMERG
FISH/NO SHALLOWS	11	11 (100%)	5.8 ± 0.7	1.3 ± 0.3	20.3 ± 2.9	15.1 ± 4.0
NO FISH/NO SHALLOWS	9	9 (100)	4.8 ± 0.8	1.6 ± 0.5	26.1 ± 5.2	23.7 ± 6.5
FISH/SHALLOWS	9	6 (67%)	4.2 ± 0.8	1.9 ± 0.3	28.7 ± 4.5	38.1 ± 6.9
NO FISH/SHALLOWS	13	8 (62%)	4.1 ± 0.5	0.9 ± 0.2	24.7 ± 4.5	43.1 ± 7.9
Total	42	34 (81%)	4.8 ± 0.4	1.4 ± 0.2	24.8 ± 2.1	30.4 ± 3.6

Permanent sites did not dry out during the course of our study. None of the non-permanent sites dried out before July 10th (conclusion of the sampling period) during either of the 2 years.

Table 2. Pond-breeding amphibians recorded in 42 replacement wetlands in the eastern Corn Belt Plains ecoregion of central Ohio.

| Species recorded		% Occurrence
American toad	*Bufo americanus americanus*	50.0
Fowler's toad	*B. fowleri*	7.1
Green frog	*Rana clamitans*	73.8
Northern leopard frog	*R. pipiens*	76.2
American bullfrog	*R. catesbeiana*	54.8
Spring peeper	*Pseudacris crucifer*	52.4
Western chorus frog	*P. triseriata*	23.8
Gray treefrog	*Hyla versicolor*	47.6
Blanchard's cricket frog	*Acris crepitans blanchardii*	11.9
Tiger salamander	*Ambystoma tigrinum*	4.8
Spotted salamander	*A. maculatum*	4.8
Small-mouthed salamander	*A. texanum*	14.3
Eastern newt	*Notophthalamus viridescens*	2.4
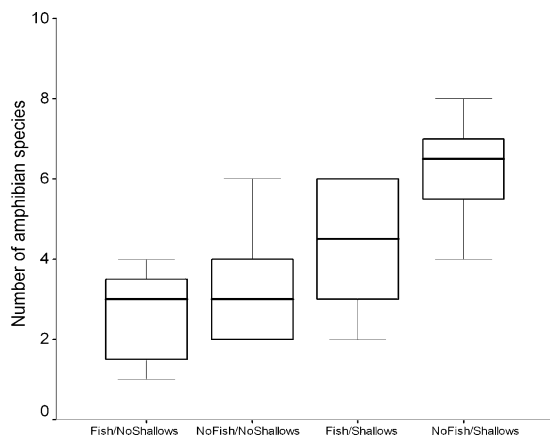
Figure 1. Box-and-whiskers plots (means, quartiles and extreme values within a category) of local amphibian species richness in 42 replacement wetlands differing in the presence of a shallow littoral zone (SHALLOWS) and presence of predatory fish (FISH) in central Ohio.

had significantly lower local species richness (average 2.63 species per site, $p = 0.02$) than all other wetland types, except for the wetlands in NO FISH/ NO SHALLOWS group. This group of study sites

also had the lowest total number of species recorded (6 species). Wetlands with shallows and without predatory fish had significantly higher average local species richness (6.16 species per site, $p < 0.01$), than all other wetland types. This group also had the highest total number of species recorded (12 species, Figures 1 and 2).

Responses of individual species

Amphibians exhibited differential responses to the presence of predatory fish and the presence of shallows (Table 3). The presence of American toads (*B. americanus*), northern leopard frogs (*Rana pipiens*), western chorus frogs (*Pseudacris triseriata*), gray treefrogs (*Hyla versicolor*) and small-mouthed salamanders (*Ambystoma texanum*) was positively associated with the presence of a shallow littoral zone in study sites. We did not have sufficient number of records to perform tests on Blanchard's cricket frogs (*Acris crepitans blanchardii*), but we recorded them only in wetlands with shallows. Although we detected no
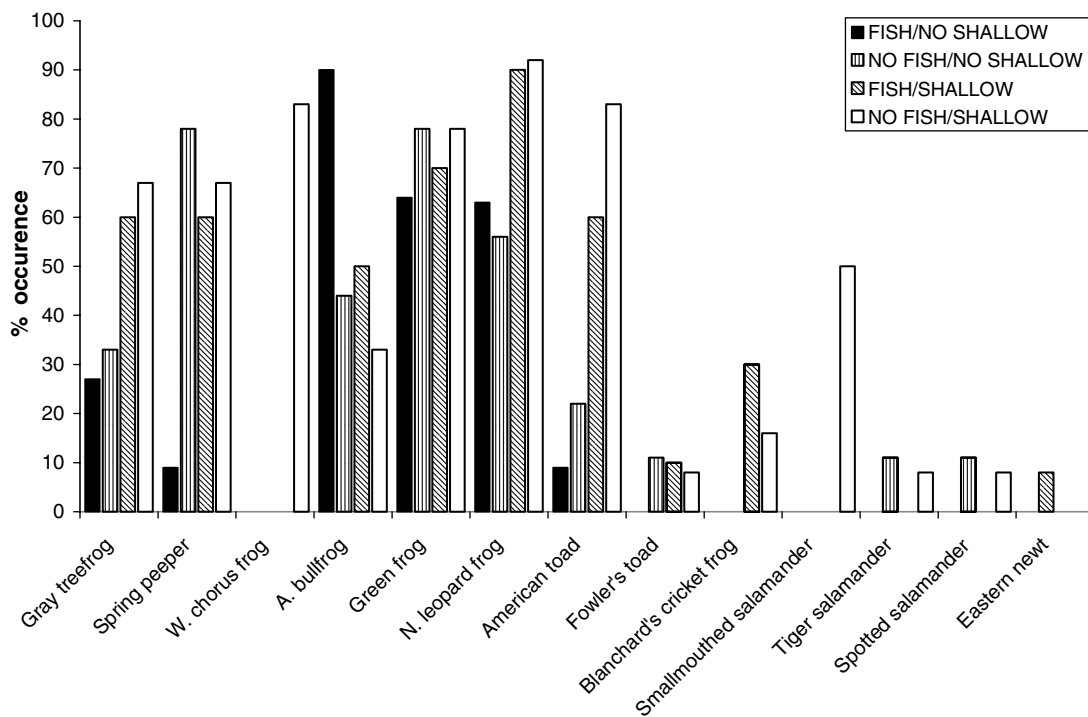

Figure 2. Distribution of amphibian species in 42 replacement wetlands in Ohio differing in the presence of predatory fish and a shallow littoral zone.
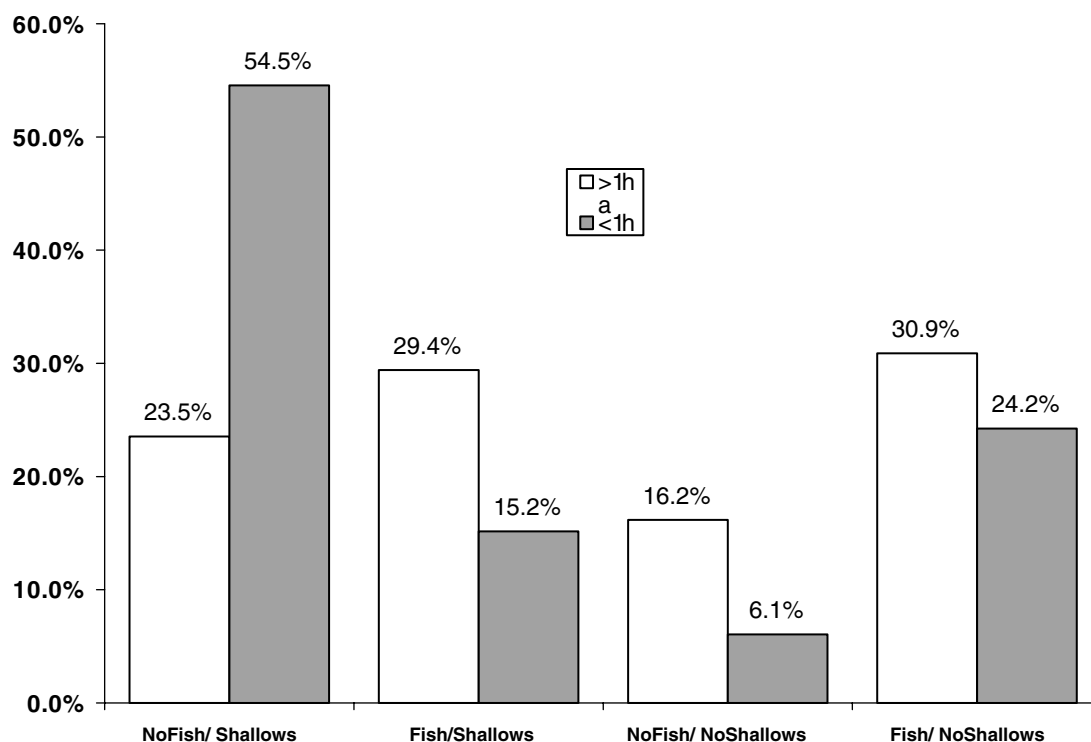
Figure 3. Distribution of 111 replacement wetlands in Ohio based on the presence of predatory fish (Fish) and the presence of a shallow littoral zone (Shallows). Sixty-eight wetlands were greater that 1 ha and 43 were less than 1 ha in size.

Table 3. Distribution of nine amphibian species in relationship to the presence of a shallow littoral zone (Shallows) and predatory fish (Fish) within 42 replacement wetlands in central Ohio.

Species	Species × Fish	Species × Shallow	Fish × Shallow	Species × Fish × Shallow	G_T
American toad	3.13	3.89* (+)	1.98	19.01**	28.05
American bullfrog	2.21	2.21	1.98	6.96*	13.10
Green frog	2.43	0.41	1.98	2.79	7.61
N. leopard frog	0.20	6.95** (+)	1.98	0.06	9.20
Spring peeper	7.25** (−)	1.98	1.98	0.63	11.84
W. chorus frog	Absent	5.28* (+)			
Gray treefrog	1.34	6.14* (+)	1.98	0.87	8.60
B. cricket frog	0.24	1.42	1.98	1.16	4.80
Small-mouthed salamander	Absent	7.28** (+)			

Values from 3-way *G*-test, except for western chorus frogs and small-mouthed salamanders that were not breeding in any wetlands with predatory fish (2-way *G*-test with Williams' correction). Positive association between species presence and variable indicated by (+), negative association by (−).

*$p < 0.05$, **$p < 0.01$ based on a chi-square distribution.

significant response to predatory fish for American toads, this species was recorded more commonly in fish-free wetlands (Species × Fish × Shallows term significant, Table 3). Spring peepers (*Pseudacris crucifer*) were recorded at all four types of wetlands, and their presence was negatively associated with presence of predatory fish. We did not record western chorus frogs and small-mouthed sala-

manders (*A. texanum*) in wetlands that contained predatory fish, regardless of whether they had shallows or not. The only two wetlands where we captured tiger salamander (*Ambystoma tigrinum*) larvae, and two others where we captured spotted salamander (*Ambystoma maculatum*) larvae, also had no predatory fish. American bullfrogs (*Rana catesbeiana*) were most common in wetlands with

predatory fish and without shallows, while green frogs (*Rana clamitans*) were ubiquitous and evenly distributed in all types of wetlands.

Predatory fish and shallows in other replacement wetlands in Ohio

Of 117 replacement wetlands constructed in Ohio since 1990, six sites had no standing water. Predatory fish were present in 60.3% of the sites greater than 1 ha, and in 39.4% of the replacement wetlands smaller than 1 ha. Overall, predatory fish were present in 52.4% of replacement wetlands constructed in Ohio. Shallow littoral zone was present at 52.9% of the replacement wetlands greater than 1 ha, and at 85.4% of the replacement wetlands less than 1 ha. Overall, shallow littoral zone was present in only 57.3% of the replacement wetlands (Figure 3).

Discussion

Our study demonstrates that the absence of a shallow littoral zone and presence of predatory fish can have a negative impact on the diversity of pond-breeding amphibians in man-made wetlands.

Hundreds of thousands of farm ponds that were used secondarily as fish ponds were constructed in the Midwest during the last century (Leja 1998; Lanoo 1996). Wetlands without a shallow littoral zone and with predatory fish present resemble gamefish ponds in design (Illinois Department of Conservation 1995), and our study demonstrates that this type of created wetland habitat is used by only a limited number of amphibian species. Amphibian communities in this wetland type were dominated by ranid frogs (American bullfrogs, green frogs and leopard frogs), with few records of spring peepers, gray treefrogs and American toads. Both American bullfrogs and green frogs produce large numbers of small eggs, possibly as an adaptation to predation (Wilbur 1984), have larvae that take a full year to develop, and are unpalatable to fish (Kats et al. 1988). Some studies have demonstrated a positive relationship between the presence of predatory fish and American bullfrogs mediated through indirect effects of fish feeding on aquatic insects, thereby lessening the predation on

bullfrog larvae (Smith et al. 1999; Adams et al. 2003). In our study, American bullfrogs were most common in pond-like wetlands containing predatory fish, a result that is consistent with previous studies (Hayes and Jennings 1986; Thurow 1994). American toad is another species whose distribution was independent of presence of predatory fish. American toad is an early colonizing species, and it is unpalatable to fish in all life stages (Licht 1968).

Ambystomatid larvae are palatable to fish (Kats et al. 1988), and centrarchid fish have been documented to cause local extirpation of small-mouthed salamander larvae (Petranka 1983). Other pond-breeding salamanders in our area may also respond to the presence of shallows and predatory fish. In ponds inhabited by bluegills, adult tiger salamanders (*A. tigrinum*) that were radio-tracked preferred shallow areas (Madison and Farrand 1998). Although interaction with fish might not be through predation, eastern newts (*Notophthalmus viridescens*) can be excluded from ponds with sunfish through competitive interactions (Smith et al. 1999).

Wetlands without shallows that do not harbor fish were used as breeding sites by a wider group of species (10 *versus* 6), but the local species richness in these wetlands remains low. However, these wetlands have a high probability of accidental or deliberate fish introductions (Porej, personal observation).

Presence of a shallow littoral zone was positively associated with presence of a number of species (American toads, western chorus frogs, leopard frogs, gray treefrogs, small-mouthed salamanders). Presence of shallows is associated with increases in amphibian diversity even in the presence of predatory fish. Although the distribution of American toads, leopard frogs, and gray treefrogs was independent of the presence of predatory fish, presence of these species was positively associated with the presence of shallows in wetlands with and without predatory fish. This result indicates that shallow littoral areas form suitable breeding sites or refugia from predators like the American bullfrog (Smith 2002), and deserves further study. If consideration is given to amphibians during the process of designing and building a replacement wetland, these data suggest that fish-free wetlands with extensive shallow littoral zones should be the preferred design.

Replacement of numerous smaller wetlands with one, larger replacement wetland may be an additional negative management strategy for wetland-dependent herpetofauna. On average, 3.11 wetlands were impacted per wetland created for individual wetland projects in our study. If we assume that both impacted and created wetlands can be approximated by either a circle or a square, conversion of 3.11 wetlands into one wetland that is 1.5 times the cumulative area of impacted wetlands (replacement ratio of 1:1.5) results in loss of over 30% of wetland/upland boundary. Wetland–upland nexus is a critical area for wetland-dependent organisms, and 'consolidation' of smaller wetlands into larger ones may further limit the functioning of replacement wetlands as quality amphibian habitat. In our study we failed to document significant association between local amphibian species richness (α-diversity) and individual wetland size, suggesting other factors such as the presence of predatory fish, a shallow littoral zone and hydroperiod are more important. Similar data exist for natural wetlands as well (Semlitsch and Bodie 1998; Snodgrass et al. 2000). Studies of other aquatic herpetofauna, such as aquatic snakes (Russel and Hanlin 1999; Roe and Kingsbury, unpublished) and turtles (Joyal et al. 2001), demonstrate that it is important to have different wetland types in close juxtaposition to provide adequate habitat for these organisms. Given the diverse habitat requirements of amphibians in our region, one type of wetland is not likely to provide adequate habitat for all species (e.g., a large, shallow, semi-permanent wetlands is not suitable habitat for American bullfrogs). We would therefore recommend that consolidation be avoided, and that several, diverse wetlands be created in lieu of one large wetland, especially if many wetlands are impacted during a project (see also Semlitsch 2000).

We did not document the presence of salamanders of the Jefferson's complex (*Ambystoma jeffersonianum*), wood frogs (*Rana sylvatica*), marbled salamanders (*Ambystoma opacum*) or four-toed salamanders (*Hemidactlium scutatum*) in any of the replacement wetlands. These species inhabit natural palustrine wetlands in central Ohio. Also, we recorded spotted salamanders and eastern newts at only two sites. All of these absent or rare species depend on the presence of upland forests to complete their life cycles (Gibbs 1998; Demaynadier and Hunter 1998; Guerry and Hunter 2002; Porej 2004). The low amounts of forest within the landscape surrounding replacement wetlands may limit the number of potential colonizers, and be insufficient to support populations of these forest-associated species (Porej et al. 2004). Disjunct distributions of these species throughout the North Central Tillplain ecoregion in Ohio indicate that most of these species were once widespread and were historically impacted by fragmentation and loss of forest habitat, including forested wetlands (Pfingsten and Downs 1989; Davis and Menze 2000). All of these species should be of some conservation concern, and careful planning of wetland design and landscape context of replacement wetlands (especially when forested wetlands are impacted) could help increase the probability of their continued survival in our region (Porej et al. 2004).

Wetland regulations and amphibian diversity

Current criteria for successful wetland creation and restoration during the 5-year post-construction monitoring period are based on the 1987 US ACoE Wetland Delineation Manual. These criteria are (a) sufficient periods of soil saturation (hydrology), (b) development of hydric soils, and (c) establishment of hydrophytic vegetation. Newly constructed wetlands with a permanent hydroperiod may have a lower risk of not satisfying the hydrology and soil criteria than a newly constructed wetland with seasonal hydrology (National Research Council 2001). A permanent hydroperiod consequently increases the probability that the site might harbor predatory fish. In addition, during a year with low precipitation, a shallow littoral zone may dry out and therefore not satisfy hydrology and soil criteria. Creation of pools with steep slopes maximizes the amount of wetland acres created per amount of land available and minimizes seasonal and year-to-year variations in the footprint of inundation (minimizing the risk of non-compliance due to insufficient wetland area created). The establishment of a narrow fringe of emergent plant species on these steep banks slopes fulfills the hydrophytic vegetation criteria (c). It is understandable then that we see an overrepresentation of open water (i.e., a single, large pool), steep slopes and permanent hydroperiods in replacement wetlands (this study, see also Galatowitsch and van der Valk 1996; Gallihugh

1998; Robb 2000; Porej 2003). This results in many wetlands providing suitable habitat for predatory fish, and a majority of them not having any shallow littoral zones, as our data on replacement wetlands in Ohio shows. Our results indicate that this traditional approach to creating and replacing wetlands has a negative impact on maintaining amphibian diversity in our region. The Ohio Environmental Protection Agency has incorporated these guidelines (replacement wetlands banks slopes 1:15 or less, no consolidation, same hydroperiods between impacted and replacement sites) into the wetland regulatory program, and we would encourage other regulatory agencies to do the same in order to avoid negative impacts to amphibian diversity through the wetland replacement process.

Acknowledgements

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